

Spathian (late Olenekian, Early Triassic) ammonoids from the Artyom area, South Primorye, Russian Far East and implications for the timing of the recovery of the oceanic environment

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Abstract. Five Spathian (late Olenekian) ammonoids are newly reported from the Zhitkov Formation in the Artyom section, South Primorye, Russian Far East. They include the early Spathian taxa *Bittnerites pacificus* and *Tirolites longilobatus* from the middle part of the formation, and *Ussuriphyllites amurensis*, *Leiophyllites* sp. and *Keyserlingites* sp. from the upper part. The *Ussuriphyllites amurensis* Zone was previously correlated with the lower Anisian, but we herein correlate it with the upper Spathian. As a consequence of this age assignment, the weakly bioturbated offshore mudstone in the middle and upper parts of the formation is correlated with the Spathian. In contrast, the Smithian (early Olenekian) offshore laminated mudstone in the lower part of the formation lacks any sign of bioturbation. These mudstones suggest that the oxygen-deficient sea floor was transformed into an aerobic environment inhabitable to benthic organisms at the Smithian-Spathian boundary.

Key words: ammonoid, bioturbation, South Primorye, Spathian, Triassic, Zhitkov Formation

Introduction

The Lower Triassic Series in South Primorye consists mainly of clastic rocks of various depositional environments and an eastward-deepening setting is inferred (Zakharov, 1968, 1997; Shigeta and Maeda, 2009). In the Russky Island-Vladivostok-Artyom area (Figure 1), shallow-marine facies of the Lower Triassic are prevalent in the southwestern part (Russky Island), while offshore facies are predominant in the northeastern part (Artyom).

The Artyom section consists of a 138-m thick, well exposed continuous succession of Triassic strata in a quarry about 8 km south of Artyom City, which is located approximately 30 km northeast of the center of Vladivostok (Figures 1, 2). The section is worthy of consideration as one of the reference sections for Triassic stratigraphy in South Primorye (Markevich and Zakharov, 2004). Previous authors recognized both the middle Smithian (early Olenekian) *Owenites* and late Smithian *Anasibirites* assemblages (Markevich and

Zakharov, 2004) and a considerable number of Smithian ammonoids have been described (Smyshlyaeva, 2010; Smyshlyaeva and Zakharov, 2012, 2013; Zakharov *et al.*, 2012, 2013; Shigeta and Kumagae, 2015). However, until now, Spathian (late Olenekian) ammonoids have not been reported.

Markevich and Zakharov (2004) claimed that sediments of Anisian age are present in the Artyom quarry as isolated tectonic klippe, which are in fault contact with Smithian sediments. As the quarry was excavated over a wider area over the last ten years, a continuous succession of Smithian and overlying younger sediments became well exposed. In this paper, we document Spathian ammonoids from the section and discuss the recovery of the oceanic environment at the Smithian-Spathian boundary based on our observations of the various mudstones of the Zhitkov Formation.

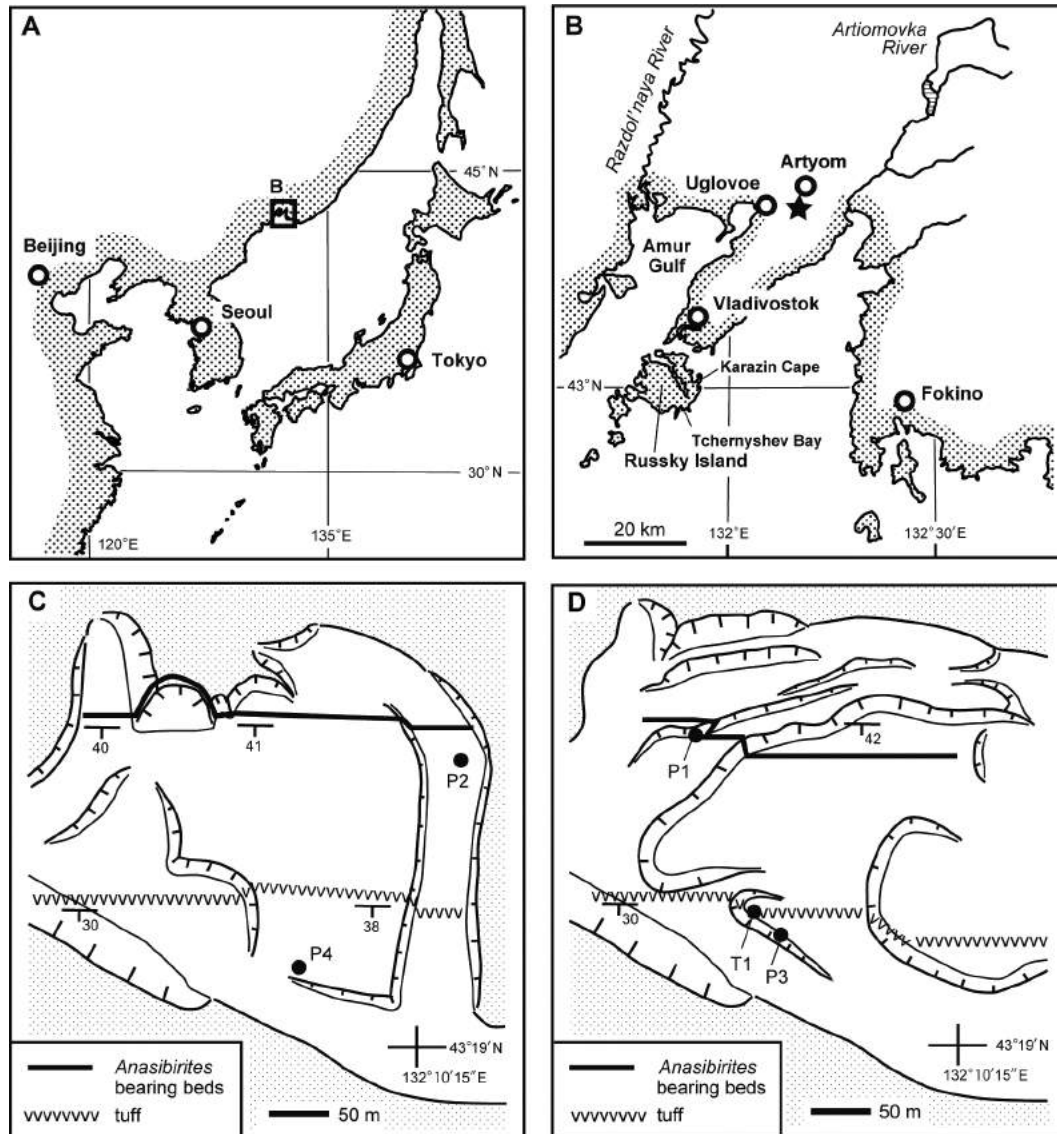


Figure 1. General map (A) showing location of South Primorye. Location (B) of the Artyom section indicated by star, and sketch maps (C, D) showing localities from which the Spathian ammonoids were collected. Quarry sketch maps C and D were made in 2005–2008 and 2011–2012 respectively. The 50–60-cm thick *Anasibirites*-bearing beds and the 30-cm thick white vitric tuff bed are widely traceable in the quarry.

Notes on stratigraphy

Lower Triassic strata in the Artyom section, which generally strike E–W and dip 25–40° southward, are divided into the Lazurnaya Bay and Zhitkov formations in ascending order. The 11-m thick Lazurnaya Bay Formation consists only of unfossiliferous muddy sandstone, whereas the overlying 127-m thick Zhitkov Formation is composed of dark grey to black laminated mudstone with intercalations of fine-grained sandstone in the lower part

(Figure 3A, B) and weakly bioturbated, dark grey to black mudstone in the middle and upper parts (Figure 3C, D). A 30-cm thick, white vitric tuff bed provides a useful lithological marker in the upper part of the section.

Ammonoids are abundant in the fine-grained sandstone beds in the lower part of the Zhitkov Formation in the Artyom section, in which the middle Smithian index ammonoid *Owenites* Hyatt and Smith, 1905, is found in the middle part and the late Smithian index ammonoid *Anasibirites* Mojsisovics, 1896, occurs in the topmost

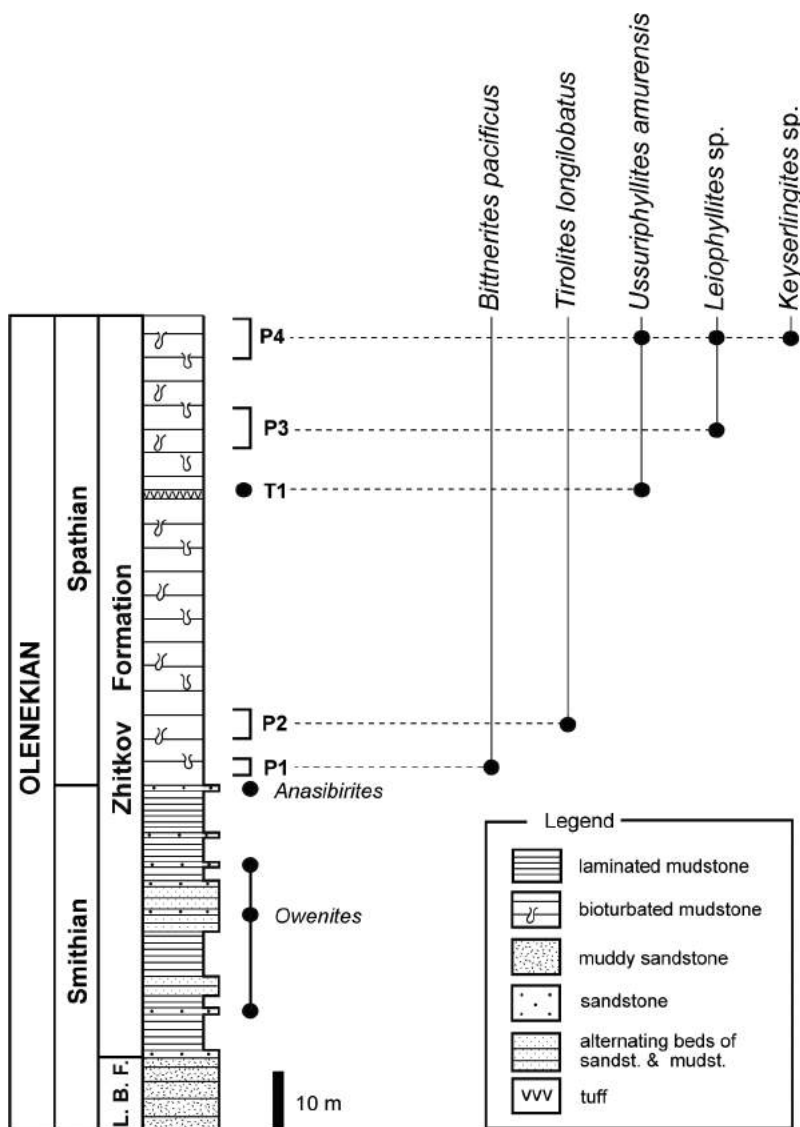


Figure 2. Lithology and stratigraphic occurrence of ammonoids in the Lower Triassic Artyom section. L.B.F.: Lazurnaya Bay Formation.

part. The widely traceable 50–60-cm thick *Anasibirites*-bearing beds are composed of sandstones and laminated mudstones.

Contrary to Markevich and Zakharov's (2004) interpretation, we have determined that sediments of the Anisian Karazin Cape Formation, which consists mainly of sandy siltstone and striped sandstone in the stratotype section at Karazin Cape, Russky Island (Zakharov, 1997), do not exist in the quarry, whether by fault contact or normal succession and furthermore, no large faults are recognized in the section.

Spathian ammonoid occurrences

The 80-m thick continuous succession of the upper Zhitkov Formation overlying the *Anasibirites*-bearing beds (Shigeta and Kumagae, 2015) in the Artyom section consists mainly of weakly bioturbated, dark grey to black mudstone (Figures 2, 3C). *Bitnnerites pacificus* Zharnikova in Buryi and Zharnikova, 1981 was collected from a float concretion found at Loc. P1, which most likely came from the lowest part of the succession. A float concretion found at Loc. P2 yielded *Tirolites longilobatus* Shevyrev, 1968. The middle part of the succession is not as fossil-

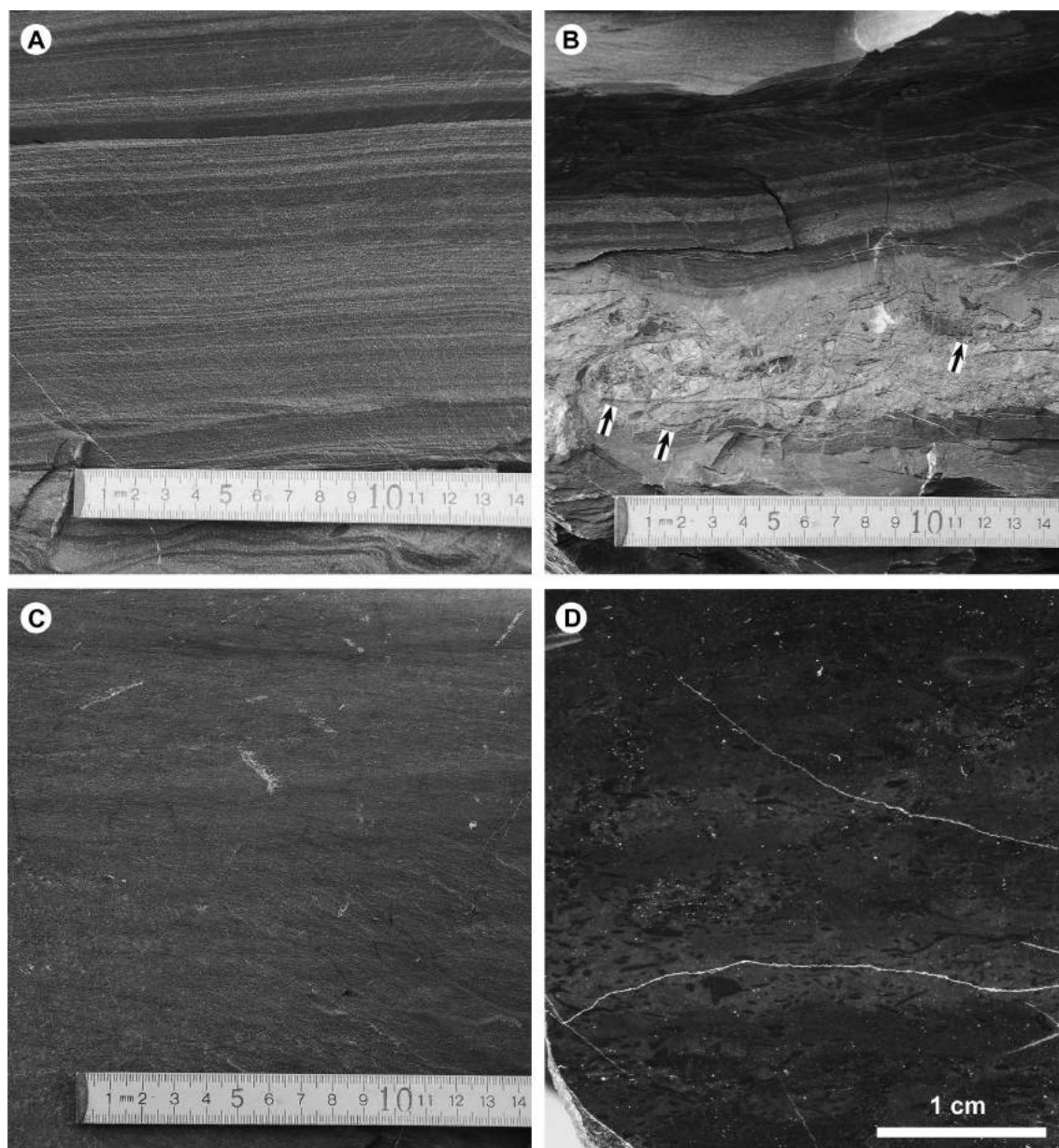


Figure 3. A, B, Mudstone with intercalations of fine-grained sandstone in the Smithian part of the Zhitkov Formation; A, Dark grey, well laminated mudstone; non-bioturbated lithology suggests a lack or near lack of benthic organisms under anoxic to dysoxic environment; B, fine-grained sandstone bed containing many ammonoids (arrows); ammonoid remains probably have been transported from their biotope to the deep basin by sediment gravity flow after death; C, D, mudstone in the Spathian part of the Zhitkov Formation; C, bioturbated, dark grey mudstone; D, vertical cross section of bioturbated mudstone; numerous mm-scale dark ovals which are small horizontal burrows of *Phycosiphon* isp., are concentrated at several levels.

iferous and has not yet yielded ammonoids. The upper part is relatively fossiliferous and ammonoids have been collected from both concretions and mudstone. A concretion found 1 cm above the 30-cm thick white vitric tuff marker bed at Loc. T1 contained *Ussuriphyllites amuren-*

sis (Kiparisova, 1961). Specimens of *Leiophyllites* sp. were collected from a float concretion as well as blocks of mudstone found at Loc. P3. In addition to *Leiophyllites* sp., *Keyserlingites* sp. and *U. amurensis* were also collected from float concretions and blocks of mudstone

at Loc. P4.

Paleontological description

Systematic descriptions basically follow the classification established by Shevyrev (1986) and in part by Tozer (1981, 1994). Morphological terms are those used in the *Treatise on Invertebrate Paleontology* (Moore, 1957). Quantifiers used to describe the size and shape of ammonoid shell replicate those proposed by Matsumoto (1954, p. 246) and modified by Haggart (1989, table 8.1).

Abbreviations for shell dimensions.—*D* = shell diameter; *U* = umbilical diameter; *H* = whorl height; *W* = whorl width.

Institution abbreviations.—CGM = Central Scientific-Research Geological Prospecting Museum (TsNIGR Museum), St. Petersburg; NMNS = National Museum of Nature and Science, Tsukuba; PIN = Paleontological Institute, Russian Academy of Sciences, Moscow.

Order Ceratitida Hyatt, 1884
Superfamily Dinaritoidea Mojsisovics, 1882
Family Tirolitidae Mojsisovics, 1882
Genus ***Tirolites*** Mojsisovics, 1879

Type species.—*Tirolites idrianus* Hauer, 1865.

Tirolites longilobatus Shevyrev, 1968

Figure 4A–H

Tirolites longilobatus Shevyrev, 1968, p. 156, pl. 10, fig. 1, text-fig. 45.

Tirolites cassianus (Questedt, 1849). Buryi and Zharnikova, 1981, p. 64, pl. 7, fig. 2, text-fig. 3.

Holotype.—PIN 1855/60, figured by Shevyrev (1968, p. 156, pl. 10, fig. 1), from the *Kiparisovites* Zone (lower Spathian) near the Dolnaya well, northern slope of the Karatauchik Ridge, Mangyshlak, Kazakhstan.

Materials examined.—One specimen, NMNS PM35051, extracted from a float concretion at Loc. P2.

Description.—Very evolute, fairly compressed shell with trapezoidal whorl section, broadly rounded venter, rounded ventral shoulders, and slightly convex flanks with maximum whorl width near ventral shoulders. Umbilicus fairly wide with gently inclined wall. Ornamentation consists of spiny tubercles on ventrolateral shoulders as well as variable strength, slightly sinuous, prorsiradiate ribs. Ventrolateral tubercles become weaker on last quarter whorl of body chamber. Suture not visible.

Measurements.—Taken at *D* = 44.0 mm of NMNS PM35051, *U* = 21.0 mm, *H* = 13.0 mm, *W* = 12.0 mm, *U/D* = 0.48, *W/H* = 0.92.

Remarks.—A specimen described as *Tirolites cassianus*

(Questedt, 1849) from Tchernyshev Bay in Russky Island, South Primorye by Buryi and Zharnikova (1981, pl. 7, fig. 2, CMG 2/10195) shows some pathological deformations of the body chamber, which is characterized by a backward bending of the ribs on the midflank and an asymmetrical whorl section. Except for the pathological deformation, its shell features closely matches *Tirolites longilobatus*.

Occurrence.—*Tirolites longilobatus* is known from the lower Spathian of Mangyshlak, Kazakhstan (Shevyrev, 1968) and Russky Island and Artyom, South Primorye (Buryi and Zharnikova, 1981).

Family Dinaritidae Mojsisovics, 1882
Genus ***Bittnerites*** Kittl, 1903

Type species.—*Tirolites (Bittnerites) bittneri* Kittl, 1903.

Bittnerites pacificus Zharnikova in Buryi and Zharnikova, 1981

Figure 4I, J

Bittnerites pacificus Zharnikova in Buryi and Zharnikova, 1981, p. 67, pl. 7, fig. 4.

Holotype.—CGM 17/10195, figured by Buryi and Zharnikova (1981, p. 67, pl. 7, fig. 4), from the *Tirolites* Zone (lower Spathian) on Tchernyshev Bay in Russky Island, South Primorye, Russia.

Materials examined.—One specimen, NMNS PM35052, extracted from a float concretion at Loc. P1.

Description.—Very evolute, fairly compressed shell with rectangular whorl section, broadly rounded venter, rounded ventral shoulders, and slightly convex flanks with maximum whorl width near mid-flank. Umbilicus fairly wide with low, vertical wall and rounded shoulders. Ornamentation on middle growth stage consists of strong, radial or slightly prorsiradiate ribs arising on umbilical shoulder and fading away on ventral shoulder. Ribs decrease in strength and become much finer on last quarter whorl of body chamber. Suture ceratitic, but not well visible.

Remarks.—Zakharov and Rybalka (1987) assigned *Bittnerites pacificus* to *Bandoites* Zakharov in Zakharov and Rybalka (1987), but the prominent ribs on the inner flank of *B. pacificus* do not support this assignment because the ribs of *Bandoites* are more distinctive on its outer flanks.

Occurrence.—*Bittnerites pacificus* is known from the lower Spathian of Artyom and Russky Island, South Primorye (Buryi and Zharnikova, 1981).

Superfamily Ceratitaceae Mojsisovics, 1879

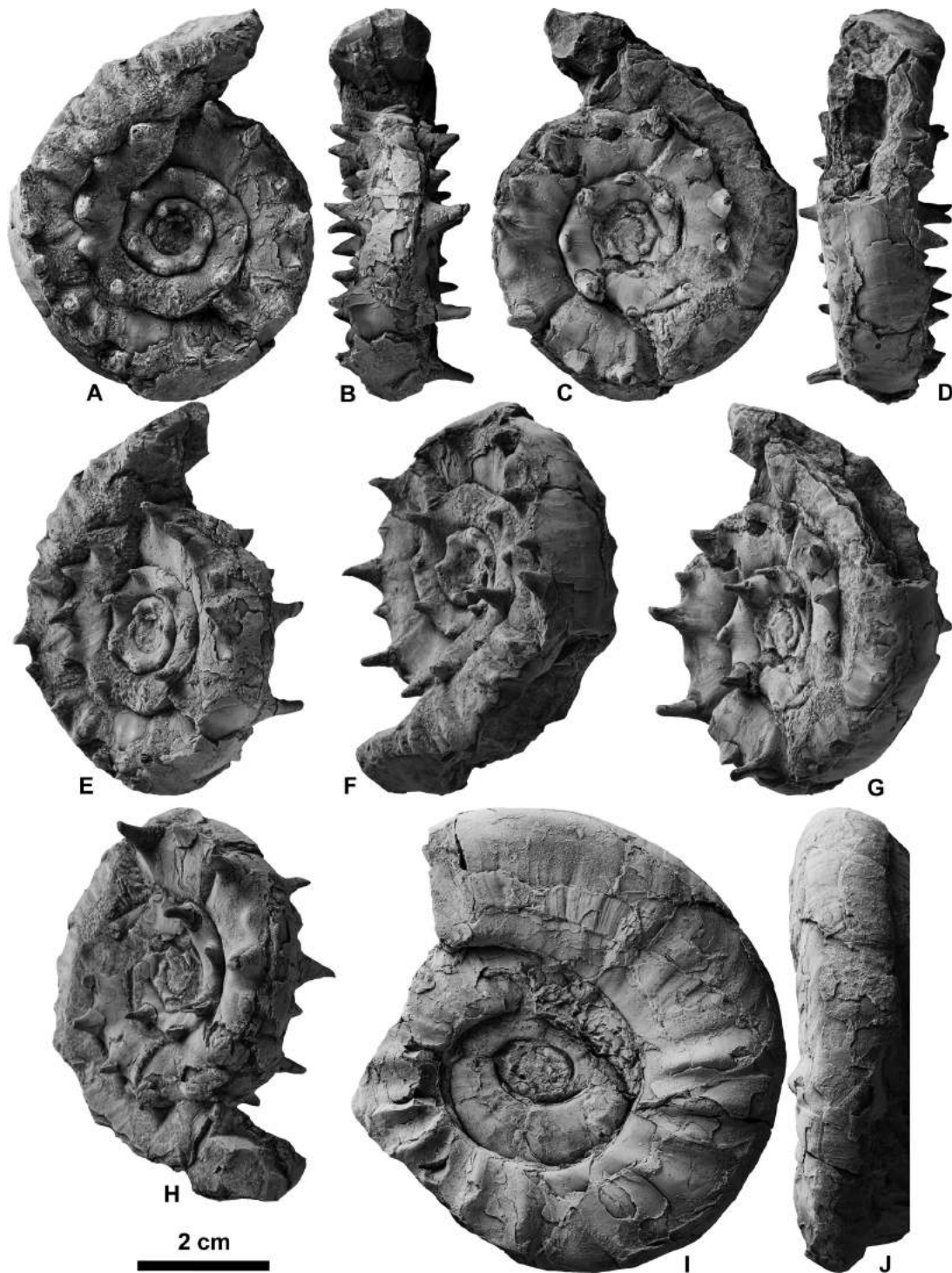


Figure 4. *Tirolites* and *Bittnerites* from the Zhitkov Formation. **A–H**, *Tirolites longilobatus* Shevyrev, 1968, NMNS PM35051 from Loc. P2; A, left lateral view; B, apertural view; C, right lateral view; D, ventral view; E, oblique apertural view, normal orientation; F, oblique ventral view, reversed orientation; G, oblique ventral view, normal orientation; H, oblique apertural view, reversed orientation; **I, J**, *Bittnerites pacificus* Zharnikova in Buryi and Zharnikova, 1981, NMNS PM35052 from Loc. P1; I, right lateral view; J, ventral view.

Family Keyserlingitoidea Zakharov, 1970

Genus **Keyserlingites** Hyatt, 1900

Type species.—*Ceratites subrobustus* Mojsisovics, 1886.

Keyserlingites sp.

Figure 5

Durgaites aff. *dieneri* (Mojsisovics, 1902). Zakharov, 1968, p. 133, pl. 26, fig. 2, pl. 27, fig. 1.

Materials examined.—Two specimens, NMNS PM35053, 35054, extracted from float concretions at Loc. P4. NMNS PM35053 (Figure 5A–C) is an incomplete specimen and NMNS PM35054 (Figure 5D, E) is a body chamber fragment.

Description.—Fairly large, moderately evolute shell, whose equal height and width results in a quadrate whorl section, broadly rounded venter, rounded ventral shoulders, and slightly convex flanks with maximum whorl width at midflank. Umbilicus fairly narrow with high, vertical wall and rounded shoulders. Ornamentation consists of robust tubercles on umbilical shoulder and small ventrolateral tubercles as well as slightly sinuous, prorsiradiate ribs of variable strength. Suture not visible.

Remarks.—The described specimens are somewhat similar to *Keyserlingites subrobustus* (Mojsisovics, 1886), but their fragmental nature precludes a definitive species assignment. A specimen from Karazin Cape in Russky Island, South Primorye attributed to *Durgaites* aff. *dieneri* (Mojsisovics, 1902) by Zakharov (1968, pl. 26, fig. 2, pl. 27, fig. 1) is very close to our described specimens and is most likely conspecific.

Occurrence.—Described specimens collected from float concretions that probably came from the *Ussuriphyllites amurensis*-bearing beds of the upper Spathian in the Artyom section.

Order Phylloceratida Zittel, 1884

Superfamily Ussuritoidea Hyatt, 1900

Family Palaeophyllitidae Popov in Luppov and Drushchits, 1958

Genus **Ussuriphyllites** Zakharov, 1967

Type species.—*Eophyllites amurensis* Kiparisova, 1961.

Ussuriphyllites amurensis (Kiparisova, 1961)

Figure 6A, B

Eophyllites amurensis Kiparisova, 1961, p. 137, pl. 28, figs. 7, 8, text-fig. 104.

Ussuriphyllites amurensis (Kiparisova, 1961). Zakharov, 1967, p. 50, pl. 4, fig. 8–10; Zakharov, 1968, p. 123, pl. 22, figs. 12, 13, pl.

23, fig. 1; Zakharov *et al.*, 2005a, fig. 3; Zakharov *et al.*, 2005b, fig. 8.

Holotype.—CGM 153/5504, figured by Kiparisova (1961, p. 137, pl. 28, fig. 8), from the *Subcolumbites* beds? on the western coast of Amur Gulf, South Primorye, Russia.

Materials examined.—One specimen, NMNS PM35055, from concretion found 1 cm above the 30-cm thick white vitric tuff marker bed at Loc. T1 (Figure 3D), and one specimen, NMNS PM35056, from a float mudstone block at Loc. P4.

Description.—Fairly involute, very compressed shell with convex flanks. Maximum whorl width at midflank, from where flank converges toward acute venter. Umbilicus fairly narrow with low, nearly vertical wall and rounded shoulders. Faint strigations visible on lateral side of shell. Suture ceratitic, but not well visible.

Occurrence.—*Ussuriphyllites amurensis* is known from the upper Spathian (beds immediately above the middle Spathian “*Subcolumbites*” *multiformis* Zone) of the Artyom section and on Russky Island and the western coast of the Amur Gulf, South Primorye (Buryi and Zharnikova, 1981; Zakharov, 1968; Zakharov *et al.*, 2005b).

Genus **Leiophyllites** Diener, 1915

Type species.—*Monophyllites suessi* Mojsisovics, 1882.

Leiophyllites sp.

Figures 6C, D, 7

Materials examined.—One specimen, NMNS PM35057, from a float concretion at Loc. P3, one specimen, NMNS PM35058, from a float block of mudstone at Loc. P3, and three specimens, NMNS PM35059–35061, from float blocks of mudstone at Loc. P4.

Description.—Very evolute, very compressed shell with elliptical whorl section, rounded venter, rounded ventral shoulders, and slightly convex flanks with maximum whorl width slightly below midflank. Umbilicus fairly wide with low, gently sloped wall and rounded shoulders. Ornamentation consists of somewhat radial or slightly rursiradiate rounded ribs arising on umbilical shoulder and fading away on ventral shoulder. Suture ceratitic, not well visible.

Remarks.—Kiparisova (1961) described a new species, *Leiophyllites praematurus*, from the *Subcolumbites* Zone on the western coast of the Amur Gulf, South Primorye. The holotype and paratype of this new taxon, which are less than 3 cm in diameter, are probably immature shells. The inner whorls of the described specimens



Figure 5. *Keyserlingites* sp. from Loc. P4 in the Zhitkov Formation. A–C, NMNS PM35053; A, left lateral view of the inner whorl; B, left lateral view; C, ventral view of A; **D, E**, NMNS PM35054; D, left lateral view; E, ventral view.

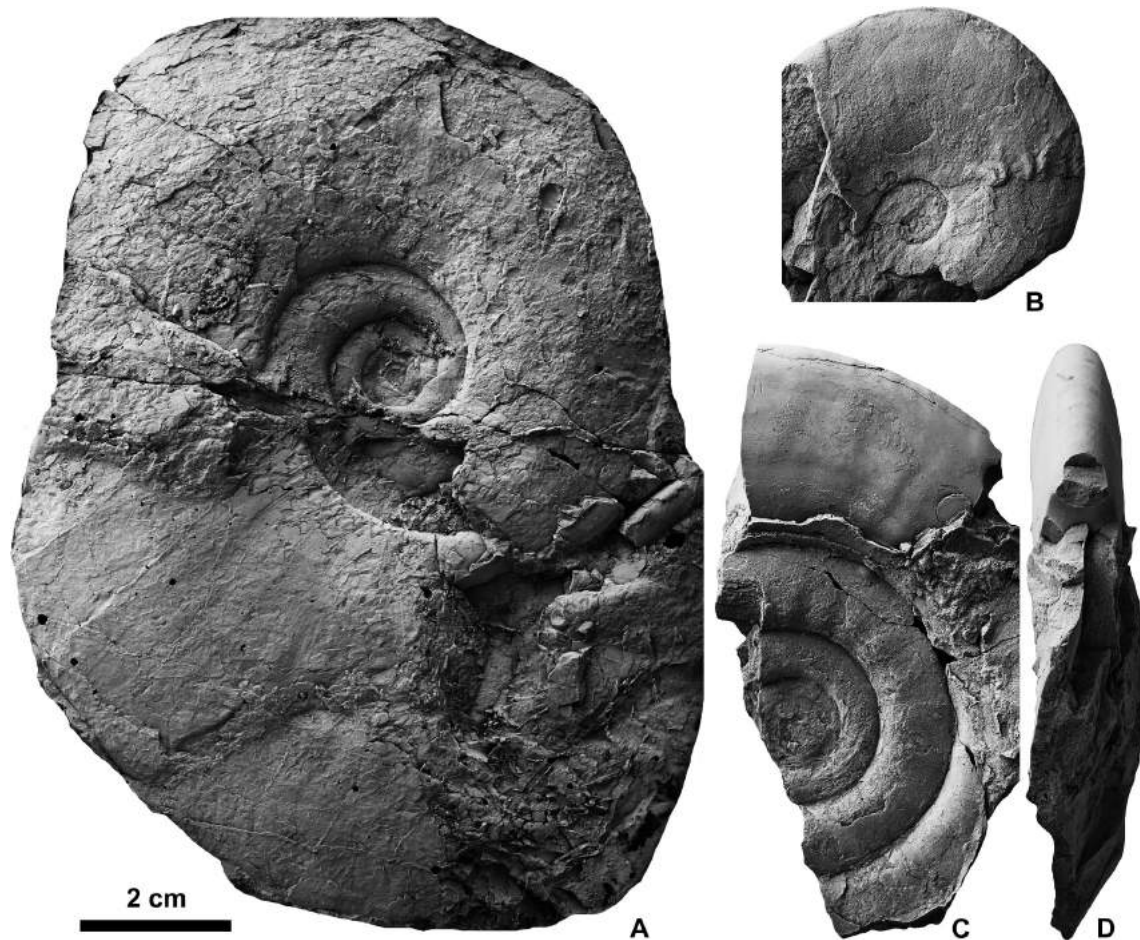


Figure 6. *Ussuriphyllites* and *Leiophyllites* from the Zhitkov Formation. **A, B**, *Ussuriphyllites amurensis* (Kiparisova, 1961); A, MNMS PM35055 (plastic cast of outer mold) from Loc. T1; right lateral view; B, MNMS PM35056 from Loc. P4; right lateral view; **C, D**, *Leiophyllites* sp., NMNS PM35059 from Loc. P4; C, right lateral view; D, ventral view.

are ornamented with slightly rursiradiate rounded ribs, which differ from *L. praematurus* with its smooth shell. However, the poor preservation of our specimens prevents a definitive species assignment.

Occurrence.—Described specimens were collected from a float concretion and float blocks of mudstone that probably came from the *Ussuriphyllites amurensis*-bearing beds of the upper Spathian in the Artyom section.

Discussion

Biostratigraphical correlation

Bittnerites pacificus was described from the *Tirolites* Zone (lower Spathian) of a section in Tchernyshev Bay on Russky Island, South Primorye by Buryi and Zharnikova (1981), who also documented the occurrence of *Tirolites cassianus* from the same 35-m thick rock unit. Their

specimen of *T. cassianus*, CMG 2/10195 is herein assigned to *T. longilobatus*. According to Shevyrev (1968), *T. longilobatus* occurs in the *Kiparisovites* Zone of the lower Spathian at Mangyshlak, Kazakhstan. The occurrences of *B. pacificus* and *T. longilobatus* in the Artyom section suggests that the lower part of the bioturbated mudstone unit immediately above the upper Smithian *Anasibirites*-bearing beds should be correlated with the lower Spathian.

The upper part of the bioturbated mudstone unit yields *Ussuriphyllites amurensis*, *Leiophyllites* sp. and *Keyserlingites* sp. The *Ussuriphyllites amurensis* Zone occurs immediately above the middle Spathian “*Subcolumbites*” *multiformis* Zone on Russky Island and the western coast of the Amur Gulf, South Primorye (Buryi and Zharnikova, 1981; Zakharov, 1968; Zakharov *et al.*, 2005a, b), and because *Keyserlingites* is a Spathian index ammonoid

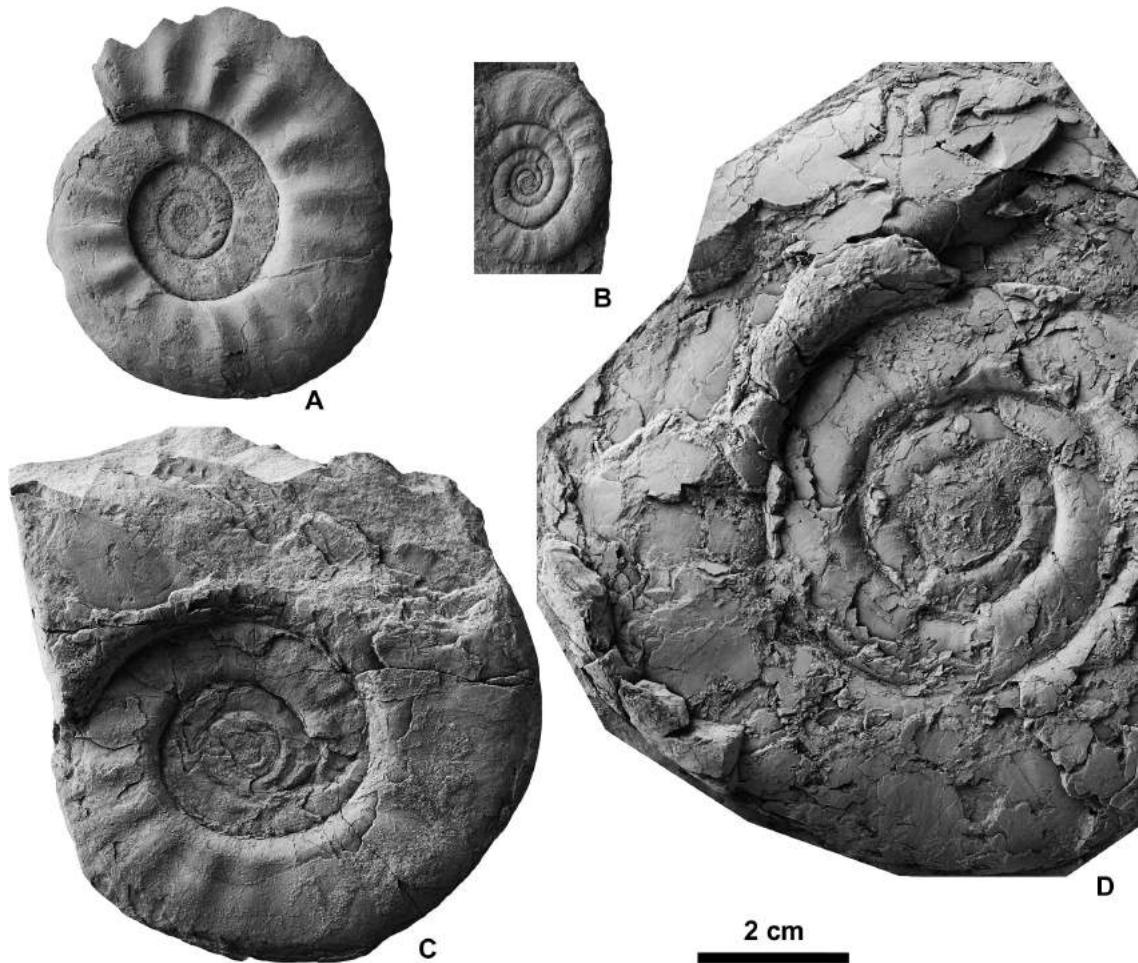


Figure 7. *Leiophyllites* sp. from the Zhitkov Formation. **A**, NMNS PM35060 from Loc. P4, right lateral view; **B**, NMNS PM35058 from Loc. P3, right lateral view; **C**, NMNS PM35061 from Loc. P4, right lateral view; **D**, NMNS PM35057 (plastic cast of outer mold) from Loc. P3, left lateral view.

(Tozer, 1965), the occurrence of *U. amurensis* and *Keyserlingites* sp. together suggests that the top part of the bioturbated mudstone unit in the Artyom section should be correlated with the upper Spathian. Zakharov and Mousavi (2013) considered the *Ussuriphyllites amurensis* Zone to be lower Anisian, but we herein regard it as late Spathian in age.

Recovery of oceanic environment

The middle and upper Smithian parts of the Zhitkov Formation in the Artyom section are composed of dark grey to black laminated mudstone with intercalations of fine-grained sandstone (Figure 3A) and pebbly sandstone. Ammonoids are abundant in those fine-grained sandstone beds (Figure 3B) that lack a coarse-grained fraction. Their sedimentary features resemble the upper

half of a Bouma sequence (Bouma, 1962) and are interpreted as distal turbidites, whose density is much lower than that of coarse-grained proximal turbidites (Reineck and Singh, 1973). The mudstones are probably suspension load deposits from low-density turbidity currents, and the numerous sandstone laminae may correspond to distal turbidites. This evidence suggests that the sediments were deposited on a submarine slope to proximal basin plain. Furthermore, the well laminated, non-bioturbated lithology of the mudstone suggests a lack or near lack of benthic organisms under anoxic to dysoxic environmental conditions (Savrdá *et al.*, 1984). In fact, no benthic fossils were found in the well laminated mudstone. Ammonoid remains in the fine-grained sandstone beds may have been transported from their biotope to the deep basin by sediment gravity flows after death (Maeda

and Shigeta, 2009).

In contrast, the Spathian part of the formation is characterized by weakly bioturbated, dark grey to black mudstone (Figure 3C, D). Small horizontal burrows of *Phycosiphon* isp. (0.5–1.0 mm diameter) are concentrated at several levels in the mudstone, and these burrows suggest the presence of an oxygenated bottom environment (Savrdá *et al.*, 1984). Sandstone beds and lens exceeding 3 cm in thickness are very few, and interbedded pebbly sandstone is absent. The decrease in abundance of relatively thick (> 5 cm thick) turbidite beds and a lack of debris flow deposits (pebbly sandstone) may suggest a deepening of the sea.

In general, dissolved oxygen levels, benthic organism diversity and burrow size decrease with increasing depth of the sea (Savrdá *et al.*, 1984). In the overlying transgressive sequence of the Artyom section, however, the bioturbated lithology becomes dominant with increasing depth of the sea. This suggests that the oxygen-deficient sea floor was transformed into an aerobic environment inhabitable to benthic organisms across the Smithian and Spathian boundary.

It is well recognized that a drastic change of marine and terrestrial ecosystems straddled the Smithian-Spathian boundary (Galfetti *et al.*, 2007). A prominent positive carbon isotope excursion known from Tethyan and Boreal marine sediments may be associated with global climate change (Payne *et al.*, 2004; Galfetti *et al.*, 2007, 2008; Horacek *et al.*, 2007; Tong *et al.*, 2007; Saito *et al.*, 2013). The reestablishment of highly diverse plant ecosystems recognized in the Barents Sea, Norway, which includes the rise of woody gymnosperms and decline of the formerly dominant lycopods, is interpreted as an effect of a major climatic change (Galfetti *et al.*, 2007). Modeling of ammonoid paleobiogeography by Brayard *et al.* (2006) suggests that the warm and equable climate during the latest Smithian was replaced by latitudinally differentiated conditions in the Spathian. The offshore mudstones in the Artyom section suggest that the bottom environment was probably deficient in dissolved oxygen during the middle and late Smithian, whereas much oxygenated bottom conditions probably resulted in active benthic behavior during the Spathian. Although it is unclear whether the oceanic environmental recovery that occurred at the Smithian-Spathian boundary was just one of a chain of episodes of global climate change, the easing of oceanic anoxia may have provided new habitats for organisms and triggered the diversification of new Mesozoic forms during the post-Early Triassic (e.g. Hallam and Wignall, 1997).

Concluding remarks

Lower Triassic strata in South Primorye record a wide range of depositional environments from nonmarine, via shoreface, to distal basin plain settings. This enables us to reconstruct the habitat for organisms as well as their oceanic environment. As demonstrated herein, the oxygen-deficient sea floor was transformed into an aerobic environment at the Smithian-Spathian boundary, even though the depositional environment became significantly deeper. Further paleoecological and paleoenvironmental studies of various lithological and depositional settings may provide an important key for understanding the global environmental changes and dynamics of the biotic recovery following the Permian-Triassic mass extinction.

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References

- Bouma, A. H., 1962: *Sedimentology of Some Flysch Deposits*, 168 p. Elsevier, Amsterdam.
- Brayard, A., Bucher, H., Escarguel, G., Fluteau, F., Bourquin, S. and Galfetti, T., 2006: The Early Triassic ammonoid recovery: paleoclimatic significance of diversity gradients. *Palaeogeography, Palaeoclimatology, Palaeoecology*, vol. 239, p. 374–395.
- Buryi, I. V. and Zharnikova, N. K., 1981: Ammonoids from the *Tiro-lites* Zone of South Primorye. *Paleontologicheskii Zhurnal*, 1981 (3), p. 61–69. (in Russian; original title translated)
- Diener, C., 1915: *Fossilium Catalogus I, Animalia, Pars 8, Cephalopoda Triadica*, 369 p. W. Junk, Berlin.
- Galfetti, T., Bucher, H., Martini, R., Hochuli, P. A., Weissert, H., Crasquin-Soleau, S., Brayard, A., Goudemand, N., Brühwiler, T. and Guodun, K., 2008: Evolution of Early Triassic outer platform paleoenvironments in the Nanpanjiang Basin (South China) and their significance for the biotic recovery. *Sedimentary Geology*, vol. 204, p. 36–60.

- Galfetti, T., Hochuli, P. A., Brayard, A., Bucher, H., Weissert, H. and Vigran, J. O., 2007: Smithian-Spathian boundary event: Evidence for global climatic change in the wake of the end-Permian biotic crisis. *Geology*, vol. 35, p. 291–294.
- Haggart, J. W., 1989: New and revised ammonites from the Upper Cretaceous Nanaimo Group of British Columbia and Washington State. *Geological Survey of Canada Bulletin*, vol. 396, p. 181–221.
- Hallam, A. and Wignall, P. B., 1997: *Mass Extinctions and Their Aftermath*, 320 p. Oxford University Press, Oxford.
- Hauer, F., 1865: Die Cephalopoden der unteren Trias der Alpen. *Sitzungsberichte der Akademie der Wissenschaften, Mathematisch-naturwissenschaftliche Klasse*, Band 52, p. 605–640.
- Horacek, M., Richoz, S., Brandner, R., Krystyn, L. and Spötl, C., 2007: Evidence for recurrent changes in Lower Triassic oceanic circulation of the Tethys: The $\delta^{13}\text{C}$ record from marine sections in Iran. *Palaeogeography, Palaeoclimatology, Palaeoecology*, vol. 252, p. 355–369.
- Hyatt, A., 1883–1884: Genera of fossil cephalopods. *Proceedings of the Boston Society of Natural History*, vol. 22, p. 253–338.
- Hyatt, A., 1900: Cephalopoda. In: Zittel, K. A. ed., *Text-book of Palaeontology*, p. 502–592. C. R. Eastman, London.
- Hyatt, A. and Smith, J. P., 1905: The Triassic cephalopod genera of America. *United States Geological Survey Professional Paper* 40, p. 1–394.
- Kiparisova, L. D., 1961: Paleontological basis for the stratigraphy of Triassic deposits of the Primorye region. 1. Cephalopod Mollusca. *Trudy Vsesoyuznogo Geologicheskogo Nauchno-Issledovatel'skogo Instituta (VSEGEI), Novaya Seriya*, vol. 48, p. 1–278. (in Russian; original title translated)
- Kittl, E., 1903: Die Cephalopoden der oberen Werfener Schichten von Muč in Dalmatien sowie von anderen dalmatinischen, bosnisch-herzegowinischen und alpinen Lokalitäten. *Abhandlungen der Geologischen Reichsanstalt (Wien)*, Band 20, p. 1–77.
- Luppov, N. P. and Drushchits, V. V., 1958: *Fundamentals of Palaeontology, Mollusca-Cephalopoda 2, Ammonoidea (Ceratites and Ammonites)*, 359 p. Gosudarstvennoye Nauchno-Tekhnicheskoye Izdatel'stvo Literatury po Geologii i Okhrane Nedr, Moscow. (in Russian; original title translated)
- Maeda, H. and Shigeta, Y., 2009: Ammonoid mode of occurrence. In: Shigeta, Y., Maeda, H., Zakharov, Y. D. and Popov, A. M. eds., *The Lower Triassic System in the Abrek Bay Area, South Primorye, Russia. National Museum of Nature and Science Monographs*, no. 38, p. 36–38.
- Markevich, P. V. and Zakharov, Y. D., 2004: *Triassic and Jurassic of the Sikhote-Alin, Book 1: Terrigenous Assemblage*, 420 p. Dalnauka, Vladivostok. (in Russian with English summary)
- Matsumoto, T., 1954: *The Cretaceous System in the Japanese Islands*, 324 p. Japan Society for the Promotion of Science, Tokyo.
- Mojsisovics, E., 1879: Vorläufige kurze Übersicht der Ammoniten-Gattungen der mediterranen und juvavischen Trias. *Verhandlungen der Kaiserlich-Königlichen Geologischen*, 1879, p. 133–143.
- Mojsisovics, E., 1882: Die Cephalopoden der mediterranen Triasprovinz. *Abhandlungen der Geologischen Reichsanstalt (Wien)*, Band 10, p. 1–322.
- Mojsisovics, E., 1886: Arktische Triasfaunen. Beiträge zur paläontologischen Charakteristik der arktischen-pazifischen Triasprovinz. *Mémoires de l'Académie Impériale des Sciences de St. Pétersbourg, sér. 7, tome 33*, p. 1–159.
- Mojsisovics, E., 1896: Beiträge zur Kenntniss der obertriadischen Cephalopoden-Faunen des Himalaya. *Denkschriften der Kaiserlichen Akademie der Wissenschaften*, Band 63, p. 575–701.
- Mojsisovics, E., 1902: Die Cephalopoden der Hallstätter Kalke. *Abhandlungen der Geologischen Reichsanstalt (Wien)*, Band 6 (Supplement), p. 177–356.
- Moore, R. C., 1957: *Treatise on Invertebrate Paleontology, Part L, Mollusca 4, Cephalopoda, Ammonoidea*, 490 p. Geological Society of America, New York and University of Kansas Press, Lawrence.
- Payne, J. L., Lehrmann, D. J., Summers, M., Wei, J. Y., Orchard, M. J., Schrag, D. P. and Knoll, A. H., 2004: Large perturbations of the carbon cycle during recovery from the end-Permian extinction. *Science*, vol. 305, p. 506–509.
- Quenstedt, F. A., 1845–1849: *Petrefactenkunde Deutschlands. Band 1. Cephalopoden*, 580 p. Ludwig Friedrich Fues, Tübingen.
- Reineck, H. E. and Singh, I. B., 1973: *Depositional Sedimentary Environments*, 439 p. Springer, Berlin.
- Saito, R., Kaiho, K., Oba, M., Takahashi, S., Chen, Z.-Q. and Tong, J., 2013: A terrestrial vegetation turnover in the middle of the Early Triassic. *Global and Planetary Change*, vol. 105, p. 152–159.
- Savda, C. E., Bottjer, D. J. and Gorsline, D. S., 1984: Development of a comprehensive oxygen-deficient marine biofacies model: Evidence from Santa Monica, San Pedro, and Santa Barbara Basin, California continental borderland. *American Association of Petroleum Geologists Bulletin*, vol. 68, p. 1179–1192.
- Shevyrev, A. A., 1968: Triassic ammonoids of the southern USSR. *Trudy Paleontologicheskogo Instituta Akademii Nauk SSSR*, vol. 119, p. 1–272. (in Russian; original title translated)
- Shevyrev, A. A., 1986: Triassic ammonoids. *Trudy Paleontologicheskogo Instituta Akademii Nauk SSSR*, vol. 217, p. 1–184. (in Russian; original title translated)
- Shigeta, Y. and Kumagai, T., 2015: *Churkites*, a trans-Panthalassic Early Triassic ammonoid genus from South Primorye, Russian Far East. *Paleontological Research*, vol. 19, p. 219–236.
- Shigeta, Y. and Maeda, H., 2009: The position of the Abrek Bay section in the “Ussuri Basin”. In: Shigeta, Y., Zakharov, Y. D., Maeda, H. and Popov, A. M. eds., *Lower Triassic System in the Abrek Bay Area, South Primorye. National Museum of Nature and Science Monographs*, no. 38, p. 36.
- Smyshlyaeva, O. P., 2010: A new species of *Euflemingites* Spath (Ammonoidea) from the Lower Triassic of South Primorye. *Paleontological Journal*, vol. 44, p. 125–128.
- Smyshlyaeva, O. P. and Zakharov, Y. D., 2012: New representatives of the family Melagathiceratidae (Ammonoidea) from the Lower Triassic of South Primorye. *Paleontological Journal*, vol. 46, p. 142–147.
- Smyshlyaeva, O. P. and Zakharov, Y. D., 2013: New members of the family Flemingitidae (Ammonoidea) from the Lower Triassic of South Primorye. *Paleontological Journal*, vol. 47, p. 247–255.
- Tong, J. N., Zuo, J. X. and Chen, Z. Q., 2007: Early Triassic carbon isotope excursions from South China: Proxies for devastation and restoration of marine ecosystems following the end-Permian mass extinction. *Geological Journal*, vol. 42, p. 371–389.
- Tozer, E. T., 1965: Latest Lower Triassic ammonoids from Ellesmere Island and northeastern British Columbia. *Geological Survey of Canada Bulletin*, vol. 123, p. 1–45.
- Tozer, E. T., 1981: Triassic Ammonoidea: classification, evolution and relationship with Permian and Jurassic forms. In: House, M. R. and Senior, J. R. eds., *The Ammonoidea. Systematic Association Special Volume 18*, p. 65–100.
- Tozer, E. T., 1994: Canadian Triassic ammonoid faunas. *Geological Survey of Canada Bulletin*, vol. 467, p. 1–663.
- Zakharov, Y. D., 1967: Some Noritaceae (ceratites) from the Triassic of the Far East. *Paleontologicheskii Zhurnal*, 1967, p. 44–51. (in Russian; original title translated)

- Zakharov, Y. D., 1968: *Lower Triassic Biostratigraphy and Ammonoids of South Primorye*, 175 p. Nauk, Moscow. (*in Russian; original title translated*)
- Zakharov, Y. D., 1970: Lower Triassic *Olenekites* and *Keyserlingites* of the Olenek River (some results of study of Ceratitida in thin sections). In, Krasnov, E. V. ed., *Triassic Invertebrates and Plants of the East USSR*, p. 5–39. Dalnevostochnyj Nauchnyj Tsentr Akademii Nauk SSSR, Dalnevostochnyj Geologicheskij Institut, Vladivostok. (*in Russian; original title translated*)
- Zakharov, Y. D., 1997: Ammonoid evolution and the problem of the stage and substage division of the Lower Triassic. *Mémoires de Géologie (Lausanne)*, vol. 30, p. 121–136.
- Zakharov, Y. D., Bondarenko, L. G., Smyshlyaeva, O. P. and Popov, A. M., 2013: Late Smithian (Early Triassic) ammonoids from the *Anasibirites nevolini* Zone of South Primorye, Russian Far East. *Bulletin of the New Mexico Museum of Natural History and Science*, vol. 61, p. 597–612.
- Zakharov, Y. D. and Mousavi Abnavi, N., 2013: The ammonoid recovery after the end-Permian mass extinction: Evidence from the Iran-Transcaucasia area, Siberia, Primorye, and Kazakhstan. *Acta Palaeontologica Polonica*, vol. 58, p. 127–147.
- Zakharov, Y. D., Popov, A. M. and Buryi, G. I., 2005a: Triassic ammonoid succession in South Primorye: 4. Late Olenekian–Early Anisian zones of the Atlasov Cape section. *Albertiana*, vol. 32, p. 36–39.
- Zakharov, Y. D., Popov, A. M. and Buryi, G. I., 2005b: Unique marine Olenekian–Anisian boundary section from South Primorye, Russian Far East. *Journal of China University of Geosciences*, vol. 16, p. 219–230.
- Zakharov, Y. D. and Rybalka, S. V., 1987: A standard for the Permian–Triassic in the Tethys. In, Zakharov, Y. D. and Onoprienko, Y. I. eds., *Problems of the Permian and Triassic Biostratigraphy of the East USSR*, p. 6–48. Dalnevostochnyj Nauchnyj Tsentr Akademii Nauk SSSR, Biologo-Pochvennyj Institut, Vladivostok. (*in Russian; original title translated*)
- Zakharov, Y. D., Smyshlyaeva, O. P. and Simanenko, L. F., 2012: Triassic ammonoid succession in South Primorye: 6. Melagathiceratid ammonoids (inner shell structure, phylogeny, stratigraphical and palaeobiogeographical importance). *Albertiana*, vol. 40, p. 28–36.
- Zittel, K. A., 1884: *Handbuch der Paläontologie: Abt. 1, Band 2*, 893 p. R. Oldenbourg, München.